



Research Article

New evidence shows that *Pocillopora* ‘*damicornis*-like’ corals in Singapore are actually *Pocillopora acuta* (Scleractinia: Pocilloporidae)

Rosa Celia Poquita-Du^{‡,§}, Chin Soon Lionel Ng^{§,‡}, Jun Bin Loo[|], Lutfi Afiq-Rosli[§], Ywee Chieh Tay^{§,‡}, Peter A Todd^{§,‡}, Loke Ming Chou[§], Danwei Huang^{‡,§}

[‡] Department of Biological Sciences, National University of Singapore, Singapore, Singapore

[§] Tropical Marine Science Institute, National University of Singapore, Singapore, Singapore

[|] School of Chemical and Life Sciences, Singapore Polytechnic, Singapore, Singapore

Corresponding author: Danwei Huang (huangdanwei@nus.edu.sg)

Academic editor: Pavel Stoev

Received: 05 Dec 2016 | Accepted: 07 Feb 2017 | Published: 13 Feb 2017

Citation: Poquita-Du R, Ng C, Loo J, Afiq-Rosli L, Tay Y, Todd P, Chou L, Huang D (2017) New evidence shows that *Pocillopora* ‘*damicornis*-like’ corals in Singapore are actually *Pocillopora acuta* (Scleractinia: Pocilloporidae). Biodiversity Data Journal 5: e11407. <https://doi.org/10.3897/BDJ.5.e11407>

Abstract

Molecular sequence data have previously revealed the existence of cryptic species associated with the *Pocillopora* ‘*damicornis*-like’ coral. Recently, this species complex has been reclassified into three species including the resurrected *P. acuta*, which appears to have a wide distribution. Morphological characteristics described for *P. acuta* are present in corals previously identified as *Pocillopora damicornis*. To determine if the *Pocillopora* ‘*damicornis*-like’ colonies on Singapore’s reefs are *P. acuta*, *P. damicornis*, or both, we examined a new collection of *Pocillopora* using mitochondrial DNA data and morphology. We also compared specimen morphologies from past collections and examined the known regional distributions of both species. Our analyses show that most *Pocillopora* ‘*damicornis*-like’ corals in Singapore are *P. acuta* instead of *P. damicornis*. Findings here are important for coral diversity records in Singapore and will help clarify distributional limits of morphologically similar *Pocillopora* species.

Keywords

biodiversity, cryptic species, distribution, museum specimens, phylogenetic analysis, *Pocillopora*

Introduction

Numerous hard coral species exhibit substantial intraspecific morphological variation (Foster 1977, Foster 1983, Veron 1995), which is observable at intracolony, intrapopulation and interpopulation levels (Best et al. 1984). Such variability can arise from genetic differences or phenotypically plastic responses to the surrounding environment (Todd et al. 2004, Pinzón et al. 2013). As coral taxonomy is largely reliant on skeletal morphology (e.g. Veron 2000), such variability can potentially blur species limits and render identification difficult.

The genus *Pocillopora* Lamarck, 1816, is of special interest as it is characterised by exceptionally high levels of phenotypic variation (Veron 2000, Flot and Tillier 2006, Schmidt-Roach et al. 2014a), and its species are frequently used as models in ecological and experimental studies. Due to a lack of clear morphological traits to distinguish among species, some taxa have historically been synonymised. For example, *Pocillopora damicornis* (Linnaeus, 1758) has had at least five synonyms (*P. acuta* Lamarck, 1816; *P. brevicornis* Lamarck, 1816; *P. bulbosa* Ehrenberg, 1834; *P. favosa* Ehrenberg, 1834; and *P. caespitosa* Dana, 1846), which are all considered to be morphological variants of a single complex associated with different environments (Veron and Pichon 1976, Veron 2000, Schmidt-Roach et al. 2013).

Recently, *P. acuta* was re-established as an entirely separate species from *P. damicornis* based on differences in their mitochondrial open reading frame (ORF) sequences (Schmidt-Roach et al. 2014a). *Pocillopora acuta* also differs from *P. damicornis* by possessing more elongated, sharper and thinner branchlets, as well as having dark brown pigmentation around the oral openings of the polyps (Schmidt-Roach et al. 2014a).

The morphological characteristics described for *P. acuta* are exhibited by corals previously identified as *Pocillopora damicornis* in Singapore. Based on this observation, we hypothesise that most of the *Pocillopora* colonies on Singapore's reefs are likely to be *P. acuta* and not *P. damicornis*. Here, we examine a range of *P. 'damicornis-like'* (*sensu* Pinzón et al. 2013) colony morphologies, their mitochondrial ORF sequences, and verify their taxonomic identity as the basis for characterisation of *P. acuta* or *P. damicornis* in Singapore.

Results of this study are important for coral diversity records in Singapore and will also help clarify the geographical range limits of morphologically closely-related *Pocillopora* species. As one of the most widespread corals on Singapore's reefs (Huang et al. 2009), these *P. 'damicornis-like'* colonies are able to settle and grow on natural reefs and even artificial

substrates such as seawalls and pontoons (Toh et al. 2017). Consequently, they are widely utilised in reef restoration research (Ng et al. 2016). Their accurate identification, whether they are *P. acuta* or *P. damicornis*, is critical for achieving species diversity targets in local and regional restoration efforts (Mace 2004, Wheeler 2004). Similar to other corals, *Pocillopora* is threatened by habitat loss and climate change, so a clear understanding of species boundaries will facilitate the conservation of species under this genus.

Materials and methods

Sixteen *Pocillopora* samples were collected from five coral reef sites across the southern offshore islands of Singapore. We focused on a wide range of colony morphologies that, following Veron and Pichon (1976) and Veron (2000), had been identified previously as *P. damicornis*. We photographed each colony in the field before part or all of it was collected. A 1-cm length of a branch was preserved in 100% ethanol while the rest of the colony sample was soaked in freshwater, bleached in 2% sodium hypochlorite, then rinsed, cleaned and dried. These samples (Fig. 1), along with others loaned from the Zoological Reference Collection (ZRC; Fig. 2) at the Lee Kong Chian Natural History Museum (LKCNHM, Singapore), were photographed and characterised according to the diagnostic characters specified by Schmidt-Roach et al. (2014a).

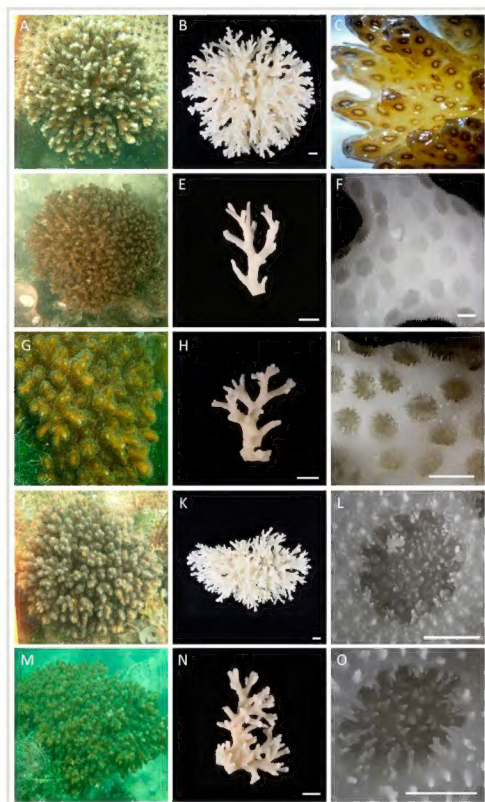


Figure 1.

Pocillopora specimens examined in this study. *In situ* appearances (A: HD159, D: HD162, G: HD161, J: HD160, M: HD154), with corresponding images of bleached skeletons (B, E, H, K, N). C, live specimen showing brown ring surrounding each oral opening (image by Jenny). F, I, branches from colonies shown in D and G respectively. L, O, calices and septa from colonies shown in J and M respectively. Scale bars represent 1 cm (B, E, H, K, N) and 1 mm (F, I, L, O) respectively.

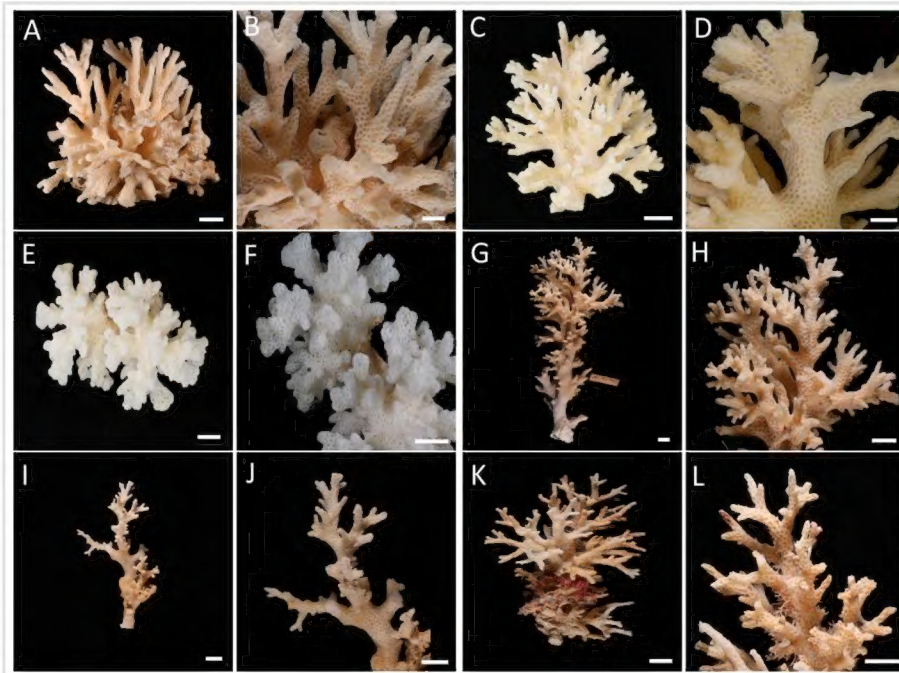


Figure 2.

Pocillopora specimens previously identified as *P. damicornis* from the Zoological Reference Collection, Lee Kong Chian Natural History Museum, Singapore (A, B: ZRC.1980.20.133; C, D: ZRC.1991.766; E, F: ZRC.1987.1538; G, H: ZRC.1987.1995; I, J: ZRC.1991.763; K, L: ZRC.1987.1537). A–F, colonies with thick branches; G–L, colonies with thinner branches. Scale bars represent 1 cm.

DNA was extracted by overnight digestion in hexadecyltrimethylammonium bromide (CTAB) and proteinase K, followed by phase separation using phenol: chloroform: isoamyl-alcohol (25:24:1). Polymerase chain reactions primed using FATP6.1 and RORF were performed according to Flot et al. (2008) for amplifying the mitochondrial open reading frame (Flot and Tillier 2007). Reaction products were purified using SureClean Plus (Bioline) and sequenced with the 3730xl DNA Analyzer (Thermo Fisher Scientific). Sequences were deposited in GenBank (accession numbers KY587458–KY587472).

We compiled in Mesquite 3.10 (Maddison and Maddison 2016) the sequences obtained here combined with 146 sequences available in GenBank (Schmidt-Roach et al. 2012, Schmidt-Roach et al. 2013, Marti-Puig et al. 2014), which were derived from *Pocillopora eydouxi* and *P. ligulata*—designated as outgroups in our analyses—as well as *P. damicornis*, *P. acuta*, *P. aliciae*, *P. verrucosa* and *P. meandrina* (Types α , β , δ , γ and m , respectively, according to Schmidt-Roach et al. 2014a). Alignments were carried out in MAFFT 7.205 using default parameters (Kato and Standley 2013, Kato and Toh 2008, Kato et al. 2002), and the 850-bp data matrix was analysed phylogenetically under maximum likelihood and Bayesian optimality criteria.

We used RAxML 8.0.9 (Stamatakis 2006, Stamatakis 2014, Stamatakis et al. 2008) for maximum likelihood analysis, generating 50 alternate runs from distinct parsimony starting trees with the default GTRGAMMA substitution model. Branch supports were assessed via 1000 replicates of bootstrap analysis. For Bayesian analysis, we first selected the most suitable evolutionary model for the data (GTR + I) using jModelTest 2.1.10 (Guindon and Gascuel 2003, Darriba et al. 2012, Posada 2008), following the Akaike information criterion

(AIC). Then, Bayesian inference was carried out using MrBayes 3.2.5 (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003, Ronquist et al. 2012), implementing six million generations of Markov chain Monte Carlo in two separate runs and saving a tree every hundredth generation. We used Tracer 1.6 (Rambaut et al. 2014) to assess convergence among the runs, and determined that the first 10001 trees were to be discarded as burn-in.

Results

Our phylogenetic analysis of seven *Pocillopora* species recovers two moderately-supported monophyletic groups of *P. meandrina* + *P. verrucosa* (*P. damicornis* type γ) and 'Clade 1', as defined by Schmidt-Roach et al. (2014a). The latter clade comprises the *P. damicornis* types α , β and δ , which correspond to the newly-delimited taxa *P. damicornis*, *P. acuta* and *P. aliciae*, respectively (Fig. 3).

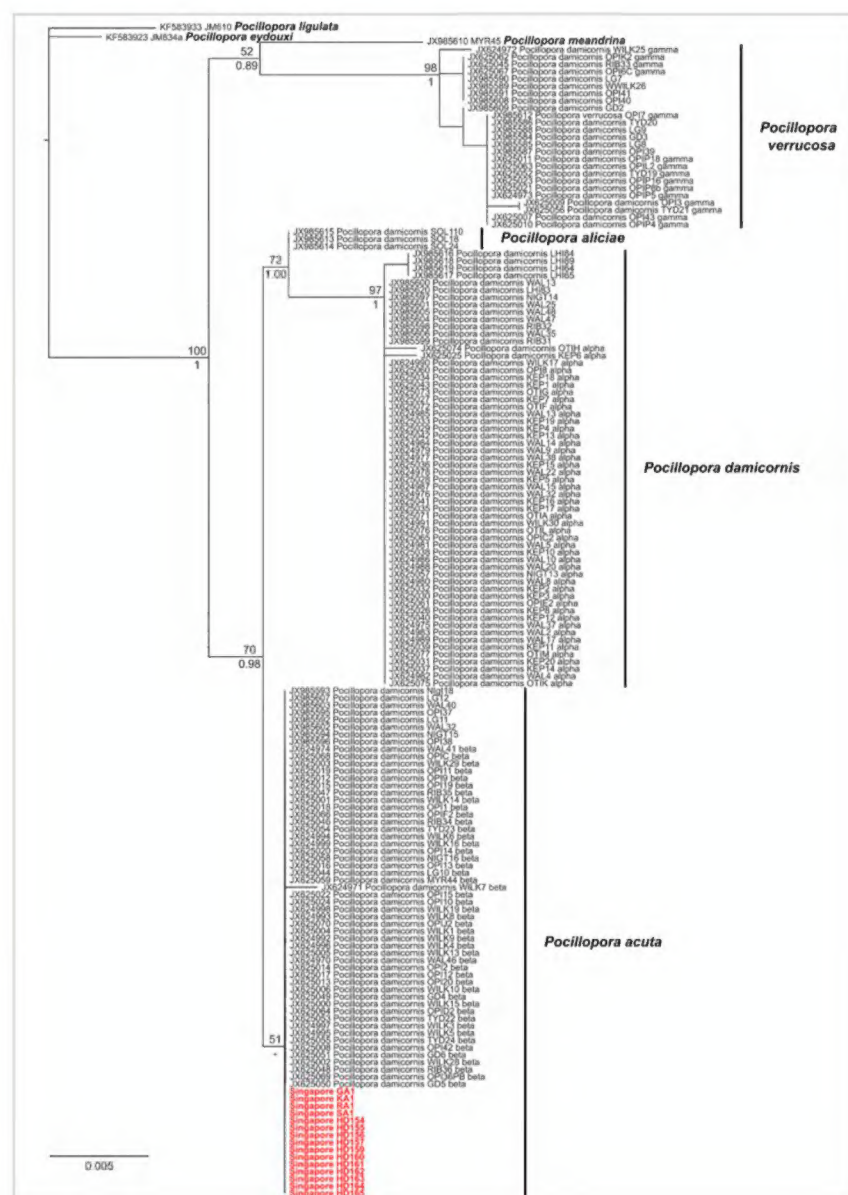


Figure 3.

Maximum likelihood tree of seven *Pocillopora* species based on the mitochondrial open reading frame. Colonies from Singapore are shown in red. Bootstrap values (≥ 50) and Bayesian posterior probabilities (≥ 0.85) are shown for supported clades.

The topology and statistical supports within this clade match those obtained by Schmidt-Roach et al. (2014a), with only the subclade of type α being highly supported. Types β and δ are only minimally supported by maximum likelihood inference and not supported by Bayesian analysis. Nevertheless, each of these sequence types are supported by nucleotide changes that are fixed within the clade. Type α sequences are distinguished from type β and type δ sequences based on six and four variable sites, respectively, while the latter two types are different at two sites across the 850-bp alignment. Therefore, sequencing errors aside, ORF sequences can help separate the three species effectively despite minimal phylogenetic supports.

***Pocillopora acuta* Lamarck, 1816**

Pocillopora acuta Lamarck, 1816, p. 274; Schmidt-Roach et al. 2014a, p. 17; Schmidt-Roach et al. 2014b, p. 11; Kitano et al. 2015, p. 21; Mayfield et al. 2015, p. 1.

Materials examined. MNHN-IK-2010-792 (holotype, Muséum national d’Histoire naturelle de Paris, France; type locality: Indian Ocean); see Table 1 for voucher specimens (ZRC, LKCNHM).

| Table 1. Voucher specimens examined. | | | | | | |
|---|---------------|--------------------|----------------------|----------------|-----------------|-------------------------------|
| Specimen no. | Catalogue no. | Locality | Latitude, Longitude | Date collected | Collector | Last identification |
| RA1 | - | Raffles Lighthouse | 1.1602°N, 103.7403°E | Oct 2015 | R.C. Poquita-Du | <i>Pocillopora damicornis</i> |
| GA1 | - | Raffles Lighthouse | 1.1602°N, 103.7403°E | Oct 2015 | R.C. Poquita-Du | <i>Pocillopora damicornis</i> |
| SA1 | - | St. John’s Island | 1.2236°N, 103.8452°E | Oct 2015 | R.C. Poquita-Du | <i>Pocillopora damicornis</i> |
| HD154 | ZRC.CNI.1067 | Pulau Subar Darat | 1.2158°N, 103.8314°E | Oct 2016 | D. Huang | <i>Pocillopora acuta</i> |
| HD155 | - | Pulau Subar Darat | 1.2158°N, 103.8314°E | Oct 2016 | D. Huang | <i>Pocillopora acuta</i> |
| HD156 | - | Pulau Subar Darat | 1.2158°N, 103.8314°E | Oct 2016 | Y.C. Tay | <i>Pocillopora acuta</i> |
| HD157 | ZRC.CNI.1068 | Pulau Subar Darat | 1.2158°N, 103.8314°E | Oct 2016 | Y.C. Tay | <i>Pocillopora acuta</i> |
| HD158 | - | Pulau Subar Darat | 1.2158°N, 103.8314°E | Oct 2016 | Y.C. Tay | <i>Pocillopora acuta</i> |
| KA1 | - | Kusu Island | 1.2257°N, 103.8602°E | Oct 2015 | R.C. Poquita-Du | <i>Pocillopora damicornis</i> |
| HD159 | ZRC.CNI.1069 | Kusu Island | 1.2257°N, 103.8602°E | Oct 2016 | C.S.L. Ng | <i>Pocillopora acuta</i> |

| | | | | | | |
|-------|-------------------|------------------|-------------------------|----------|-------------------------|-------------------------------|
| HD160 | ZRC.CNI.1070 | Kusu Island | 1.2257°N, 103.8602°E | Oct 2016 | C.S.L. Ng | <i>Pocillopora acuta</i> |
| HD161 | ZRC.CNI.1071 | Pulau Subar Laut | 1.2126°N, 103.8334°E | Oct 2016 | Y.C. Tay | <i>Pocillopora acuta</i> |
| HD162 | ZRC.CNI.1072 | Pulau Subar Laut | 1.2126°N, 103.8334°E | Oct 2016 | Y.C. Tay | <i>Pocillopora acuta</i> |
| HD163 | - | Pulau Subar Laut | 1.2126°N, 103.8334°E | Oct 2016 | Y.C. Tay | <i>Pocillopora acuta</i> |
| HD164 | - | Pulau Subar Laut | 1.2126°N, 103.8334°E | Oct 2016 | Y.C. Tay | <i>Pocillopora acuta</i> |
| HD165 | - | Pulau Subar Laut | 1.2126°N, 103.8334°E | Oct 2016 | Y.C. Tay | <i>Pocillopora acuta</i> |
| - | ZRC.1980.3.20.133 | Sentosa | - | Sep 1979 | L.T. Chan | <i>Pocillopora damicornis</i> |
| - | ZRC.1987.1537 | Pulau Hantu | - | 1987 | L.M. Chou | <i>Pocillopora damicornis</i> |
| - | ZRC.1987.1538 | Pulau Hantu | - | 1987 | L.M. Chou | <i>Pocillopora damicornis</i> |
| - | ZRC.1991.763 | Pulau Hantu | - | 1991 | Reef Ecology Study Team | <i>Pocillopora damicornis</i> |
| - | ZRC.1991.766 | Singapore | - | 1991 | Reef Ecology Study Team | <i>Pocillopora damicornis</i> |
| - | ZRC.1987.1995 | Singapore | - | - | Reef Ecology Study Team | <i>Pocillopora damicornis</i> |

Description. Colonial, densely caespitose (Fig. 1A, D, G, J, M); branches typically round in cross section, but may become flattened at the tips, which are usually sharply pointed. Branches of colonies in exposed sites thicken and have smaller spacing between branches (Fig. 2A–F), while those in sheltered sites are elongate and slender (Fig. 2G–L). Calices typically oval, with the small diameter ranging between 0.6 and 0.8 mm, and the large diameter between 1.0 and 1.2 mm. Columellae flat. Septa poorly developed, in two equal cycles; 12 septa per corallite (Fig. 1L, O). Coenosteum with fine spinules. Living colony pale-greenish in colour with characteristic darker pigmentation surrounding oral opening of polyps (Fig. 1C).

Remarks. Colonies collected from Singapore's reefs show great variation in branching morphologies, overlapping with those described for *Pocillopora acuta* and *P. damicornis* by Schmidt-Roach et al. (2014a). For instance, *Pocillopora acuta* colonies observed from exposed environments in Singapore have considerably thicker branches (~6 mm) than those shown in Schmidt-Roach et al. (2014a). The pigmentation rings may not be clearly visible for all corallites in every colony; they vary from faint to intense brown. Nevertheless, sequences of the mitochondrial open reading frame from these colonies are all nested within the type-β clade that has been redefined as *P. acuta* (Schmidt-Roach et al. 2014a). The bootstrap support and posterior probability are low, but our sequences exactly match

(100% identity) nearly all the published *P. acuta* sequences obtained from Australia and Japan (Fig. 3).

Discussion

This study contributes to the limited data that have emerged from the South China Sea region on the identity of *Pocillopora* species. The recently-revived species *P. acuta* is described to have a wide distribution reaching from the central Pacific to the Indian Ocean (Schmidt-Roach et al. 2014a). Our results show clearly the presence of *Pocillopora acuta* in Singapore, one of the southernmost localities in the South China Sea. Here, it is found in nearly every offshore reef (Huang et al. 2009), and colonies are common in the shallows (0–4 m below chart datum) but generally do not exist beyond 6 m depth. They thrive in various types of habitats including on artificial substrates such as seawalls and pontoons (Toh et al. 2017), and serve as habitat for diverse ectosymbiont communities (Lee and Sin 2009). The species is hermaphroditic (Kerr et al. 2011) and has been documented to brood monthly in Singapore, just before or after the new moon (Chou and Quek 1993, Toh et al. 2013).

Although we find no contemporary evidence of *P. damicornis* on Singapore's reefs, the variability of colony branch thickness among specimens from past collections held at the LKCNHM (Fig. 2) appears greater than those collected from the field for this study and overlaps with that of *P. damicornis* as defined by Schmidt-Roach et al. (2014a). Nevertheless, some specimens we sequenced as *P. acuta* here, which were collected from several environments spread across most of the reef localities in Singapore, also had thick branches and rounded tips (e.g. HD154; Fig. 1M, N) diagnostic of *P. damicornis* (Schmidt-Roach et al. 2014a). This wide morphological variation appears to be associated with wave and current exposure, with an increase in branch thickness going from sheltered sites to more exposed ones. It is also possible that the actual *P. damicornis* species had been present before but faced recent losses locally due to pressures from coastal development (Chou 2006, Huang et al. 2009). Hence, a regional investigation with genetic samples from less impacted reefs may help clarify the historical distributions of *P. acuta* and *P. damicornis*.

The taxonomy of South China Sea *Pocillopora* remains poorly understood. A previous study has shown that *Pocillopora* 'damicornis-like' types 4 and 5 are present in Taiwan, while the Gulf of Thailand only hosts the latter type (Pinzón et al. 2013). More recently, these genetic types 4 and 5 have been delimited as *Pocillopora damicornis* (type α) and *P. acuta* (type β) respectively by Schmidt-Roach et al. (2013), Schmidt-Roach et al. (2014a). These findings were based on the mitochondrial ORF, the same marker we have sequenced here, thus underlining its utility as a reliable method of identifying the *Pocillopora* species present in Singapore.

Broadly, *Pocillopora acuta* is present in both Taiwan and Gulf of Thailand, but *P. damicornis* appears to be limited to the northern South China Sea as it has thus far only been

confirmed from Taiwan using the mitochondrial ORF. Further north at the Yaeyama Islands, Japan, *P. damicornis* is present but is likely rare relative to *P. acuta* (Kitano et al. 2015). Despite that, *P. damicornis* is the only *Pocillopora* species detected along mainland Japan to date (Pinzón et al. 2013). All these sequencing work, applied on a wide range of colony and corallite morphologies that overlap with both species (Figs 1, 2), suggests that *P. damicornis* is rare in the South China Sea and southern Japan.

Thus far ranging from the Central Pacific to the Indian Ocean through Singapore, Taiwan and Hawai'i, further sampling may reveal the presence of *P. acuta* in more localities in the Central Indo-Pacific. Overall, the emerging picture shows that most 'damicornis-like' corals in the southwestern South China Sea region are actually *P. acuta* instead of *P. damicornis*.

Acknowledgements

This study is funded by the National Research Foundation (Singapore) through the Marine Science R&D Programme (R-154-000-A25-281). We thank Bert Hoeksema and an anonymous reviewer for helping to improve the manuscript, and Chua Keng Soon (LKCNHM) for assistance with loans, imaging and cataloguing of specimens.

References

- Best MB, Boekschoten GJ, Oosterbaan A (1984) Species concept and ecomorph variation in living and fossil Scleractinia . *Palaeontographica Americana* 54: 70-79. URL: <http://archive.org/details/palaeontographic541984pale>
- Chou LM (2006) Marine habitats in one of the world's busiest harbours. In: Wolanski E (Ed.) *The Environment in Asia Pacific Harbours*. Springer, The Netherlands, 377-391 pp. https://doi.org/10.1007/1-4020-3655-8_22
- Chou LM, Quek ST (1993) Planulation in the scleractinian coral *Pocillopora damicornis* in Singapore waters. *Proceedings of the 7th International Coral Reef Symposium* 1: 500.
- Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9 (8): . <https://doi.org/10.1038/nmeth.2109>
- Flot J, Tillier S (2006) Molecular phylogeny and systematics of the scleractinian coral genus *Pocillopora* in Hawaii. *Proceedings of the 10th International Coral Reef Symposium* 24-29.
- Flot J, Tillier S (2007) The mitochondrial genome of *Pocillopora* (Cnidaria: Scleractinia) contains two variable regions: The putative D-loop and a novel ORF of unknown function. *Gene* 401: 80-87. <https://doi.org/10.1016/j.gene.2007.07.006>
- Flot J, Magalon H, Cruaud C, Couloux A, Tillier S (2008) Patterns of genetic structure among Hawaiian corals of the genus *Pocillopora* yield clusters of individuals that are compatible with morphology. *Comptes Rendus Biologies* 331: 239-247. <https://doi.org/10.1016/j.crvi.2007.12.003>

- Foster AB (1977) Patterns of small-scale variation of skeletal morphology within the scleractinian corals, *Montastrea annularis* and *Siderastrea siderea*. Proceedings of the Third International Coral Reef Symposium 2: 409-415. URL: http://www.reefbase.org/resource_center/publication/pub_22034.aspx
- Foster AB (1983) The relationship between corallite morphology and colony shape in some massive reef-corals. Coral Reefs 2: 19-25. <https://doi.org/10.1007/BF00304728>
- Guindon S, Gascuel O (2003) A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. Systematic Biology 52 (5): 696-704. <https://doi.org/10.1080/10635150390235520>
- Huang D, Tun KPP, Chou LM, Todd PA (2009) An inventory of zooxanthellate scleractinian corals in Singapore, including 33 new records. Raffles Bulletin of Zoology Supplement 22: 69-80. URL: <http://rmbr.nus.edu.sg/rbz/biblio/s22/s22rbz069-080.pdf>
- Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17 (8): 754-755. <https://doi.org/10.1093/bioinformatics/17.8.754>
- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology and Evolution 30 (4): 772-780. <https://doi.org/10.1093/molbev/mst010>
- Katoh K, Toh H (2008) Recent developments in the MAFFT multiple sequence alignment program. Briefings in Bioinformatics 9 (4): 286-298. <https://doi.org/10.1093/bib/bbn013>
- Katoh K, Misawa K, Kuma K, Miyata T (2002) MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acids Research 30 (14): 3059-3066. <https://doi.org/10.1093/nar/gkf436>
- Kerr AM, Baird AH, Hughes TP (2011) Correlated evolution of sex and reproductive mode in corals (Anthozoa: Scleractinia). Proceedings of the Royal Society B-Biological Sciences 278 (1702): 75-81. <https://doi.org/10.1098/rspb.2010.1196>
- Kitano YF, Nagai S, Ueno M, Yasuda N (2015) Most *Pocillopora damicornis* around Yaeyama Islands are *Pocillopora acuta* according to mitochondrial ORF sequences. Galaxea 17 (1): 21-22. <https://doi.org/10.3755/galaxea.17.21>
- Lee AC, Sin TM (2009) *Trapezia septata* Dana, 1852 (Brachyura, Trapeziidae): a new record for Singapore with notes on its relationship with the host coral, *Pocillopora verrucosa*. Crustaceana 82 (12): 1603-1608. <https://doi.org/10.1163/156854009X463838>
- Mace GM (2004) The role of taxonomy in species conservation. Philosophical Transactions of the Royal Society B: Biological Sciences 359 (1444): 711-719. <https://doi.org/10.1098/rstb.2003.1454>
- Maddison WP, Maddison DR (2016) Mesquite: A Modular System for Evolutionary Analysis (Version 3.10). URL: <http://mesquiteproject.org>
- Marti-Puig P, Forsman ZH, Haverkort-Yeh RD, Knapp ISS, Maragos JE, Toonen RJ (2014) Extreme phenotypic polymorphism in the coral genus *Pocillopora*; micro-morphology corresponds to mitochondrial groups, while colony morphology does not. Bulletin of Marine Science 90 (1): 211-231. <https://doi.org/10.5343/bms.2012.1080>
- Mayfield AB, Bruckner AW, Chen C, Chen C (2015) A survey of pocilloporid corals and their endosymbiotic dinoflagellate communities in the Austral and Cook Islands of the South Pacific. Platax 12: 1-17.

- Ng CSL, Toh TC, Chou LM (2016) Coral restoration in Singapore's sediment-challenged sea. *Regional Studies in Marine Science* 8: 422-429. <https://doi.org/10.1016/j.rsma.2016.05.005>
- Pinzón JH, Sampayo E, Cox E, Chauka LJ, Chen CA, Voolstra CR, LaJeunesse TC (2013) Blind to morphology: genetics identifies several widespread ecologically common species and few endemics among Indo-Pacific cauliflower corals (*Pocillopora*, Scleractinia). *Journal of Biogeography* 40: 1595-1608. <https://doi.org/10.1111/jbi.12110>
- Posada D (2008) jModelTest: Phylogenetic model averaging. *Molecular Biology and Evolution* 25 (7): 1253-1256. <https://doi.org/10.1093/molbev/msn083>
- Rambaut A, Suchard MA, Xie D, Drummond AJ (2014) Tracer: MCMC Trace Analysis Tool. Version 1.6. URL: <http://beast.bio.ed.ac.uk/Tracer>
- Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19 (12): 1572-1574. <https://doi.org/10.1093/bioinformatics/btg180>
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61 (3): 539-542. <https://doi.org/10.1093/sysbio/sys029>
- Schmidt-Roach S, Miller KJ, Lundgren P, Andreakis N (2014a) With eyes wide open: a revision of species within and closely related to the *Pocillopora damicornis* species complex (Scleractinia; Pocilloporidae) using morphology and genetics. *Zoological Journal of the Linnean Society* 170 (1): 1-33. <https://doi.org/10.1111/zoi.12092>
- Schmidt-Roach S, Johnston E, Fontana S, Jury CP, Forsman Z (2014b) Daytime spawning of *Pocillopora* species in Kaneohe Bay, Hawai'i. *Galaxea* 16: 11-12. <https://doi.org/10.3755/galaxea.16.11>
- Schmidt-Roach S, Miller KJ, Woolsey E, Gerlach G, Baird AH (2012) Broadcast spawning by *Pocillopora* species on the Great Barrier Reef. *PLoS ONE* 7 (12): . <https://doi.org/10.1371/journal.pone.0050847>
- Schmidt-Roach S, Lundgren P, Miller KJ, Gerlach G, Noreen AME, Andreakis N (2013) Assessing hidden species diversity in the coral *Pocillopora damicornis* from Eastern Australia. *Coral Reefs* 32 (1): 161-172. <https://doi.org/10.1007/s00338-012-0959-z>
- Stamatakis A (2006) RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22 (21): 2688-2690. <https://doi.org/10.1093/bioinformatics/btl446>
- Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30 (9): 1312-1313. <https://doi.org/10.1093/bioinformatics/btu033>
- Stamatakis A, Hoover P, Rougemont J (2008) A rapid bootstrap algorithm for the RAxML web servers. *Systematic Biology* 57 (5): 758-771. <https://doi.org/10.1080/10635150802429642>
- Todd PA, Ladle RJ, Lewin-Koh NJI, Chou LM (2004) Genotype × environment interactions in transplanted clones of the massive corals *Favia speciosa* and *Diploastrea heliophora* . *Marine Ecology-Progress Series* 271: 167-182. <https://doi.org/10.3354/meps271167>
- Toh KB, Ng CSL, Wu B, Toh TC, Cheo PR, Tun K, Chou LM (2017) Spatial variability of epibiotic assemblages on marina pontoons in Singapore. *Urban Ecosystems* 20: 183-197. <https://doi.org/10.1007/s11252-016-0589-2>

- Toh TC, Peh JWK, Chou LM (2013) Heterotrophy in recruits of the scleractinian coral *Pocillopora damicornis* . Marine and Freshwater Behaviour and Physiology 46 (5): 313-320. <https://doi.org/10.1080/10236244.2013.832890>
- Veron JEN (1995) Corals in Space and Time. UNSW Press, Sydney, 320 pp.
- Veron JEN (2000) Corals of the World. Australian Institute of Marine Science, Townsville, 1381 pp.
- Veron JEN, Pichon M (1976) Scleractinia of Eastern Australia. Part I. Families Thamnasteriidae, Astrocoeniidae, Pocilloporidae . 1. Australian Institute of Marine Science, Townsville, 85 pp. URL: <http://archive.org/details/ScleractiniaEas00JENVB>
- Wheeler QD (2004) Taxonomic triage and the poverty of phylogeny. Philosophical Transactions of the Royal Society B: Biological Sciences 359 (1444): 571-583. <https://doi.org/10.1098/rstb.2003.1452>